Inheritance of Resistance to Tomato Yellow Leaf Curl Virus in Tomatoes

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ABSTRACT

The inheritance of resistance to the whitefly-borne tomato yellow leaf curl virus (TYLCV) in tomato was studied in progenies derived from crosses between a TYLCV-homozygous resistant line of *Lycopersicon pimpinellifolium*, LA121, and the susceptible cultivar Pearson of *L. esculentum*. Inoculations were made by means of the vector, the tobacco whitefly (*Bemisia tabaci*). Genetic data obtained from the F_1, F_2, F_3 and backcross generations indicated incomplete dominance of resistance over susceptibility, agreeing with a monogenic control of resistance. Transmission tests by means of whiteflies to *Datura stramonium* suggested that lower virus concns may have been present in plants of the resistant parent than in the susceptible Pearson tomatoes.

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Additional key words: transmission frequency and transmission efficiency of whiteflies, TYLCV symptoms.

Tomato cultivars (*Lycopersicon esculentum* Mill.) are markedly affected in Israel by a disease incited by the tomato yellow leaf curl virus (TYLCV) (1). TYLCV is not transmitted mechanically; its vector is the tobacco whitefly (*Bemisia tabaci* Gennadius) (1,2).

Cohen and Nitzany (2) studied the host range of TYLCV and reported that *L. pimpinellifolium* (Jusl.) Mill. and *L. peruvianum* (L.) Mill. were symptomless carriers of the virus; however, the accession numbers of the tested material were not indicated. In previous work (Cohen and Pilowsky, *unpublished*), plants of a large number of *L. esculentum* cultivars and breeding lines were tested for disease resistance but all proved to be susceptible. Results of further tests with wild relatives of *L. esculentum* indicated that several accessions of *L. pimpinellifolium, L. peruvianum,* and *L. chilense* Dun. carry high levels of resistance to TYLCV. Although *L. peruvianum* and *L. chilense* are distinguished from the cultivated tomato by severe compatibility barriers, and difficulty has been experienced in obtaining interspecific seed, no barriers exist to the hybridization of *L. pimpinellifolium* with *L. esculentum* and interspecific seed are readily obtained (3). A highly resistant accession of *L. pimpinellifolium* was therefore chosen as the source of TYLCV resistance in local breeding work. This paper presents the results of tests to determine the inheritance of resistance to TYLCV in accession LA121 of *L. pimpinellifolium*.

MATERIALS AND METHODS.—Seeds of *L. pimpinellifolium*, accession LA121, from the collection of C. M. Rick, Univ. of California, Davis, were furnished by Dvora Lapushner, The Volcani Center, Bet Dagan.

A TYLCV-homozygous resistant line of LA121 was used as the resistant parent, and the tomato cultivar 'Pearson' was used as the susceptible parent. Reciprocal crosses were made to obtain seeds of the F_1, F_2, and F_3 generations. F_1 hybrids were backcrossed to LA121 and to Pearson. Seeds of the first generation following the backcrosses to the susceptible and resistant parents (BC_1F_2 populations) were also obtained.

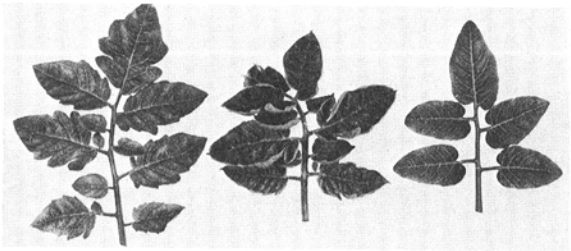

Fig. 1. Reaction of tomato genotypes following inoculation with tomato yellow leaf curl virus: left, leaf of heterozygous plant showing interveinal chlorosis; center, leaf of homozygous susceptible plant with leaflets cupped upwards: and right, symptomless leaf of homozygous resistant plant.

Plants of the above-mentioned groups were grown in 7-cm diam plastic pots in an insect-proof greenhouse and sprayed weekly with a 1% nicotine sulfate solution. Maintenance and work with the whiteflies were the same as those described previously (1). TYLCV was maintained on *Datura stramonium* L. plants, which were used as a source of inoculum. The viral inoculum was renewed every 3-4 wk. When the first true leaves were expanding, the tomato seedlings were inoculated in a constant temp chamber at 28 ± 2 C. The following inoculation procedure was used: each seedling was placed inside a plastic cylinder (3-cm diam, 5-cm high), covered with a net. Twenty viruliferous whitefly females reared on TYLCV-infected *D. stramonium* plants for 48 h, were placed in each cylinder. This population of whiteflies is greater than the number of insects required to ensure 100% transmission (2). The whiteflies were allowed to feed on the tomato seedlings for 72 h, after which the plastic cylinders were removed. The plants were then sprayed with insecticide and transferred to the greenhouse, where they were kept until the end of the trials. The final disease record was taken 8 wk after inoculation. Genetic data were analyzed by the chi-square test.

Symptomless plants were tested for infectivity on healthy *D. stramonium* plants which TYLCV infects systemically. Possible differences in virus concn in plants of the parental lines were examined on *D. stramonium*, by testing the transmission frequency and transmission efficiency of whiteflies fed on TYLCV-infected tomato plants of both genotypes.

Two terms employed in this paper are defined as follows: "Transmission frequency": The percentage of whiteflies that actually transmitted the virus, out of the total number of individuals used in the trial and which survived for 3 days or more. "Transmission efficiency": The number of transmissions established by individual inoculative whiteflies during the test period.

Data on the transmission frequency of whiteflies were analyzed by the "Sign test" (4). Results of the transmission efficiency tests were analyzed by the "Mann-Whitney U test" (5); $\alpha = 0.05$ was chosen for both of the analytical tests mentioned.

RESULTS.—*TYLCV reaction of parental lines and F_1 hybrids.*—In all trials, 100% of the Pearson plants became infected. Three classes of plants, resistant, intermediate, and susceptible, were observed following inoculations with TYLCV (Fig. 1). Susceptible plants were generally stunted. Their leaflets exhibited severe interveinal chlorosis and were markedly reduced in size and cupped upward. Plants of the resistance source, LA121, showed leaf vein-clearing, sometimes followed by a slight interveinal chlorosis soon after inoculation. Symptoms usually did not appear on newer leaflets. Periodic assays of resistant plants to *D. stramonium* indicated the presence of TYLCV. Infected F_1 hybrid plants had slightly smaller, sometimes downward-cupped leaflets that developed interveinal chlorosis (intermediate reaction). There were no apparent differences in disease reactions between reciprocal F_1 crosses (Table 1).

Reaction of F_2 and BC_1F_1 plants.—When F_2 progenies were inoculated with TYLCV, the three

TABLE 1. Reaction of F_1, F_2, and backcross (BC) progenies from crosses between *Lycopersicon pimpinellifolium* 'LA121' and *L. esculentum* 'Pearson', to tomato yellow leaf curl virus (TYLCV)

Generation	Parental line or cross	Number of plants				
		Total	Resistant	Intermediate	Susceptible	P value
P_1	LA121[a]	164	164[c]	0	0	
P_2	Pearson[b]	182	0	0	182	
F_1	LA121 × Pearson	96	0	96	0	
F_1	Pearson × LA121	83	0	83	0	
F_2	F_1 selfing	446	106	221	119	0.50-0.70
BC_1F_1	(Pearson × LA121) × Pearson	119	0	57	62	0.50-0.70
BC_1F_1	(LA121 × Pearson) × Pearson	172	0	87	85	0.80-0.90
BC_1F_1	(Pearson × LA121) × LA121	118	62	56	0	0.50-0.70

[a]Homozygous resistant parent.

[b]Homozygous suceptible parent.

[c]Expected ratio of resistant: intermediate: susceptible is 1:2:1 for F_2 generation, 0:1:1 for backcross to susceptible parent, and 1:1:0 for backcross to resistant parent.

classes (resistant, intermediate, and susceptible) were observed in a ratio of 1:2:1. Backcross progenies to the susceptible parent, Pearson, segregated in a ratio of 1 intermediate: 1 susceptible. Plants of backcross to the resistant parent, LA121, segregated in a ratio of 1 resistant: 1 intermediate (Table 1). These data suggest incomplete dominance of a single factor for TYLCV resistance.

Reaction of F_3 and BC_1F_2 generations.—The F_2 and backcross data suggested that (i) resistant progenies were homozygous for resistance, (ii) plants classified as intermediate were heterozygous for resistance, and (iii) susceptible progenies were true-breeding for susceptibility. To check this hypothesis further, a total of 39 progenies derived from selfing individual F_2 and BC_1F_1 plants selected at random from each class, were tested for resistance. Thirteen progenies grown from selfing resistant individuals were all classified as resistant following TYLCV inoculation. All 16 progenies derived from plants of the intermediate class produced the classes resistant, intermediate, and susceptible in a ratio of 1:2:1. When progenies derived from selfing 10 susceptible plants were inoculated, only susceptible individuals were observed. Thus, these results support the hypothesis that resistance to TYLCV is incompletely dominant and governed by a single gene.

Virus recovery tests from resistant and susceptible plants.—As already mentioned, TYLCV inoculation of homozygous resistant plants resulted in the absence of symptoms on new-growth leaflets. It was desired to determine the transmission frequency and the transmission efficiency of whiteflies when fed on TYLCV-resistant and susceptible plants.

Ten plants of each parent line which had been inoculated 8 wk earlier, were used as a source of inoculum for each of the following tests: five virus-free whitefly females enclosed in a leaf cage were allowed to feed for 48 h on each tomato plant. Thereafter, the whiteflies were placed singly on healthy *D. stramonium* plants for inoculation periods of 48-72 h. Later, each whitefly was transferred at intervals of 48-72 h to a new test plant for four additional transfers. In all of the six trials summarized in Table 2 the transmission frequency of whiteflies fed on resistant plants was lower than that of insects fed on susceptible plants. The difference was significant ($P = 0.016$).

Of the total number of insects employed in the transmission frequency tests, 20 inoculative whiteflies which were fed on resistant plants and 34 inoculative whiteflies which were fed on susceptible plants survived until the end of the trials. During that period the mean number of transmissions per insect (2.5) was higher in females fed on TYLCV-infected susceptible plants than in those fed on resistant plants (1.7). The differences were significant ($P = 0.02$). The results of the above-mentioned trials indicate that a difference may exist in the TYLCV concn of the two tomato genotypes.

DISCUSSION.—TYLCV-homozygous resistant

TABLE 2. Transmission frequency of whiteflies after feeding on resistant (LA121) and susceptible (Pearson) plants inoculated with tomato yellow leaf curl virus (TYLCV)

Test No. and group[a]	Number of whiteflies surviving for 3 days or more	Transmission frequency	Difference between transmission frequencies of LA121 and Pearson[b]
1 LA121	17	64.7	−29.4
1 Pearson	17	94.1	
2 LA121	21	38.0	−12.0
2 Pearson	24	50.0	
3 LA121	22	45.4	−26.8
3 Pearson	18	72.2	
4 LA121	11	45.4	−49.5
4 Pearson	20	95.0	
5 LA121	40	90.0	−6.2
5 Pearson	27	96.2	
6 LA121	24	4.1	−95.9
6 Pearson	26	100.0	

[a]Plants of each line were inoculated 8 wk before transmission tests.

[b]Significant at 5% level.

plants of *L. pimpinellifolium*, accession LA121, are characterized by a lack of symptoms on new-growth leaflets following inoculation, and by positive assays on *D. stramonium*. Plants of parent lines, F_1 hybrids, F_2, F_3, BC_1F_1, and BC_1F_2 generations were classified as resistant, intermediate or susceptible according to external disease symptoms. The class intermediate was designated to denote the reaction of F_1 hybrid plants. Further genetic data of the F_2, F_3 and backcross populations confirmed that the intermediate reaction occurred only in heterozygous plants. The segregation pattern obtained with these groups was consistent with the hypothesis that resistance to TYLCV is incompletely dominant and controlled by a single gene (Table 1).

The type of high resistance to TYLCV found in *L. pimpinellifolium*, LA121 plants, as far as visible symptoms are concerned, raises the question as to the virus content of these plants. In the present work, the evaluation of TYLCV concn based on the transmission frequency (Table 2) and on the transmission efficiency of whiteflies reared on resistant and susceptible plants, suggests that lower virus concns occur in the resistant LA121 plants than in the susceptible Pearson plants.

The level of resistance in LA121 plants appears to be sufficient to make this accession suitable as a source of TYLCV resistance. Results obtained from field trials indicated that LA121 plants were highly resistant to TYLCV when grown under severe virus infection in the Jericho area (Pilowsky and Zimmerman, *unpublished*).

The occurrence of a significant reduction in disease resistance in the heterozygous F_1 compared with that of the homozygous resistant parent may be of considerable importance in the production of TYLCV-resistant F_1 hybrid tomatoes. In such a breeding program, not only one but both parents of the hybrid combination would be required to carry the resistance factor to ensure a high degree of protection in the resulting F_1 hybrid.

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